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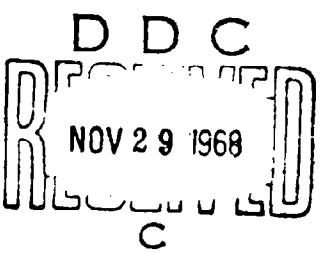

DEPARTMENT OF THE ARMY
Fort Detrick
Frederick, Maryland

CONTRIBUTION TO THE PROCESS OF LEAF FALL

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We know that the spontaneous detachment of leaves from their axes is a phenomenon which can be observed in ligneous and herbaceous plants of many kinds as a reaction to very different extrinsic and intrinsic factors and under varying circumstances. Intrinsic reasons not connected directly with the change of ambient conditions cause aging leaves to drop and are manifested in partial leaf fall (Ref. 1). The effect of extrinsic conditions becomes apparent in "summer leaf fall" (Ref. 1), in "heat leaf fall," in the petal drop investigated in Ref. 1, and in many other cases (Ref. 1).

In some years, we also observe that leaves inhabited by Cynipidae become detached from the trees in very large numbers ahead of time and without any discoloration, (Populus after infection by Pemphigus spirothece, P. bursarius and P. marsupialis; Ulmus after infection by Tetraneuri ulmi; etc. (Ref. 2). The gallnuts of Oligotrophus bursarius produced on the leaves of Glechoma and spontaneously detached upon "ripening" indicate that even parts of a leaf blade may become detached, under abnormal conditions, in the same manner, i.e. after formation of the same abscission layer which is normally formed between leaf and axis (Ref. 3).

A further form of leaf fall which can be easily induced experimentally in many plants and has already been repeatedly treated in literature is the one which occurs after mutilation and specifically after complete removal of the leaf blade. The

findings from this intervention will be reported in the following on the basis of numerous tests.

The number of plants which, after removal of the leaf blade, drop their stems within a short time after the intervention even in summer or generally under external conditions which in themselves would not cause or promote any separation of the leaves, is very large. Under equal conditions and specifically the same season, the principal difference is the interval which elapses between blade removal and stem drop. Varieties of Urtica, Impatiens parviflora, a great many varieties of Coleus hybridus and others drop the stems after mutilation within forty-eight or seventy-two hours or even earlier. Mirabilis jalapa, Alnus viridis and other varieties of Alnus, Syringa vulgaris, Symphoricarpus racemosus, Polygonum cuspidatum and Datura tatula were observed by me to drop their blade-less stems after ninety-six hours. Approximately one week elapsed with the stems of Hedera helix, Populus alba, etc. whereas Ficus carica, Ricinus communis, Viburnum opulus, etc. did not drop their stems until the start of the second week.

These indications should be amplified by noting that all of the respective tested series were made at the beginning of August in the open air. At other seasons, the intervals are different and the intervals in the air of the laboratory are shorter than in the open air. Like the blossoms of many plants, the blade-less stems become detached strikingly quickly in laboratory air. The action of the laboratory air can be further reinforced by additive gaseous contamination (Ref. 4).

From many viewpoints, I consider Coleus particularly suitable for experimental treatment of the problems of leaf-stem drop here discussed. It involves potted plants of moderate size which are easily handled. It is also of great importance that the blade-less stems of the Coleus shoot permit propagation of the reaction in a strictly acropetal direction, i.e. those of the oldest internodes drop first and then the next younger in regular sequence. Detachment of the blade-less stems does not occur in such regular sequence in all families. I observed, in Mirabilis jalapa, Datisca cannabina, etc., that the leaf stems become more easily detached at the upper parts of the shoot where blossoms already exist than at the purely vegetative lower sections of the plant. In some other plants, indeterminable individual particularities of the internodes, i.e. factors varying from one stem to the next

according to unknown laws, apparently play a large role so that the drop of the blade-less stems may take place in an entirely irregular sequence. (Observation on Polygonum cuspidatum, Populus alba, etc.). The acropetal sequence is very noticeably disturbed also in Acer pseudoplatanus. A number of observations lead me to assume that light conditions have a decisive influence on mountain maple but these observations were not further pursued.

A further advantage of working with Coleus plants results because the blade-less stems drop very quickly -- from twelve hours to a few days after mutilation -- in the moist air of the greenhouse.

In short-interval tests, the detachment of the stems in many other plants is observed at the older parts of the shoot and detachment ceases and/or appreciably slows down even at a considerable distance from the vegetation point of the main shoot whereas the phenomenon progresses in Coleus hybridus as far as the youngest internodes.

These and other advantageous properties are diminished by the fact that the plants bred as Coleus hybridus vary greatly and that these variations expressed in the dimension, nervation and particularly in the coloring of the leaf blades, is also manifested in the ease and rapidity with which the blade-less stems are detached.

From a comparison of plants of different colors, I was able to determine that anthocyanin-rich plants generally retain their leaf stems longer than anthocyanin-free plants. In green (and/or white-green) individual plants, I observed the stems drop within twenty-four or forty-eight hours under the same condition in which some red individuals retain them three, four, five days and even longer. In the following reports on my findings, there will frequently be contained an indication of the form employed. However, these indications are invalidated to a certain extent by the fact that the relation between the degree of anthocyanin content of the respective variety and of the interval elapsed until leaf-stem separation represents only a general rule and exceptions from the latter appear to be fairly frequent.

What is the effective agent after removal of the leaf blades in our tests and what changes does the operation cause in the stems or axes which lead to the detachment of the blade-less stem?

The leaf blade is the main locus of assimilation and simultaneously a very strongly transpiring structure. It would seem obvious to assume the process of stem detachment to have a causal relation with the cessation of assimilation and transpiration.

I. The relation of leaf-stem drop to the assimilation activity of the blade can be easily examined. Deprivation of light of the leaf blades does not produce the rapid detachment of the stems following removal of the blade so that we may conclude that the cessation of assimilation is not the decisive factor in the effects of blade removal.

1. Deprivation of light to the leaf blades was produced by placing the blades in black-paper bags. In several plants, only one blade each of the pairs of leaves was deprived of light and, on the opposite side, the blade removed. Whereas the blade-less stems became detached after two or three days, the blades in the dark remained firmly attached. In one individual, I observed blades in the dark become detached after eight days but otherwise they were retained longer. After two weeks, the tests on varieties with different colors were terminated when the findings remained the same.

It is also possible in another manner and without deprivation of light to eliminate any activity of assimilation. Individual plants of Coleus hybridus raised from standard commercial seed are nearly all mottled. Both the anthocynin-rich as well as the anthocyanin-free or -poor varieties have leaf blades with a wedge-shaped chlorophyll-free or -poor field broadening toward the bases of the leaf. If the green parts of the leaf are cut away so that only the pale wedge-shaped inner part remains, the stems are retained in the axis for a prolonged duration.

2. Resection of the green-blade components of mottled leaves was made on varieties with different anthocyanin content with the same result. The stems of the mutilated

leaves remained attached to the axes for a long time. Only those where the leaf remainder starts to rot, become detached very soon (the pale parts of mottled leaves have lesser resistance to putrefactive agents than the green areas). Stems of leaves aged already at the start of the test dropped off during the interval of observation. The tests were terminated after fourteen days.

II. We now turn to examination of the influence of reduced transpiration on the process of stem detachment after blade removal. We may reliably assume that the flow of transpiration in the fascicules of the stems has an appreciably diminished intensity and it is conceivable that the interruption and/or diminishing of this flow creates conditions which induce or accelerate the formation of an abscission layer at the base of the leaf stem.

What occurs if we reduce and/or diminish the intensity of transpiration without removing the leaf blades, and what occurs if we promote the flow of transpiration in bladeless stems? Vapor discharge by non-mutilated leaves was diminished in various ways.

3. Shoot sections of Coleus plants of many varieties were placed under water. Detachment of the leaves did not occur. The reaction of the plants was observed for more than one week until rotting terminated the test.

4. Robust Coleus plants were cut, the leaf blades removed and the plants then placed under water upright. Detachment of the blade-less stems took place under water appreciably slower than in air. In a green-white individual with leaves speckled slightly red, the first (lowest) stem was observed to drop after three days, the next one after four, and another one after five days. Rotting terminated the test after seven days and before the other stems had dropped off. In red individuals, all leaf stems were retained for more than one week. Ten days after start of the test, a red individual was transferred from water to the air whereupon the blade-less stems became detached within a few days.

In both tests, we must take into account the possibility that the contact with water and/or the deprivation

of oxygen of the base of the leaf stem prevented the detachment of the leaf or delayed it further after blade removal than under normal circumstances, i.e. for internodes exposed to the air. These considerations necessitated the following tests.

5. Some Coleus plants were treated so that only their shoots were submerged into water whereas the leaf stems remained exposed to the air. After the shoots had been kept in water for several days, there occurred occasionally perceptible discolorations of the anthocyanin-rich parts but the shoots remained alive and no detachment took place. In a light-green large-leaved variety (amply speckled with red), the leaf blades remained under water twelve days without becoming detached. Subsequently the blades were removed and the expected leaf drop occurred after two days.

6. Laboratories frequently utilize melted cocoa butter for diminishing transpiration by coating the plant organs with the former. Shoots of Coleus plants of many different color mixtures were treated in this manner. All varieties investigated responded with the same reaction in which the coated leaves became detached only late and repeatedly simultaneous with the non-treated but, in the majority of cases, later than the non-coated leaves. In a number of plants, the blades were cut so that only a small triangular remainder was left. The lowest aging leaves then began with the process of detachment. In many individuals, I observed that the drop of the non-coated leaves began twenty-four hours after the operation and was terminated forty-eight hours later whereas the coated leaves began to drop only forty-eight hours after the application. In other individuals, the difference was similar but became noticeable only several days after the application. The tests were made in the moist atmosphere of greenhouses.

An attempt was made further to determine the influence of vapor discharge by blade-less stems.

7. Thick-leaved individuals with robust long stems had their blades removed. The stems of the mutilated pairs of leaves were treated differently by introducing one of the two stems into a test tube whereas the other remained exposed to the open air. Most of the tests were carried out in the open

at a point protected from the sun and accessible to the wind, with varieties of different coloration. The test tubes contained a pad of moist cotton. At the base of the stem, the opening of the test tube was closed by dry cotton. The test method attempted to place the stems in moist air but to leave the point at which separation takes place, in relatively dry air. The test tubes were attached so that their weight exerted no influence on the stems.

The tests did not furnish concordant findings. In some cases, the protected and the unprotected stems were observed to become detached simultaneously. In other cases, the stems kept in moist air were retained longer than the non-protected stems in a definitely demonstrable manner. It is necessary to stress this last finding since it is confirmed by the findings from similar tests.

8. Some of the stems of blade-less leaves received black-paper caps and others without such caps were kept under normal conditions of transpiration. The detachment of the protected stems took place perceptibly slower than that of the non-protected stems. The weight of the paper caps on the stems is of no significance since control tests with non-protected but weight-loaded stems did not disclose any effect of the mechanical loading.

9. Even more striking was the effect of covering the leaf stems with tin foil. The experimental plants (plants with a light-red leaf center) clearly indicated that the non-protected stems become detached more easily than the protected stems. The time differential may amount to more than twenty-four hours. In every case, I observe the detachment also of the younger internodes in non-protected stems as compared to protected stems.

Some further tests were intended to disclose the influence of increased transpiration.

10. We utilize individuals which were raised as slips from the same plant and therefore could be regarded as similar in constitution. The tests were made in a dry cooled greenhouse. The specimens were placed under glass bells after pot and soil surface had been sealed vapor-tight. Several

dishes with calcium chloride were placed with each plant. The effect was very rapid when employing the rapidly reacting yellow-green specimens. The calcium-chloride specimens all dropped their stems within the first forty-eight hours whereas the others retained their leaves longer. Corresponding findings were obtained with red Coleus plants. In dry air, detachment occurred several days earlier than in the normal moist air.

11. An attempt was made to replace the missing blades by attached lumps or plates of gypsum and so to permit an artificial flow of transpiration through the blade-less stems. The tests were made with numerous specimens of different coloring in the greenhouse (Ref. 5). From the findings of the tests above, it might have been expected that a similar acceleration of leaf-stem detachment would occur in the stems with gypsum lumps, due to the better transpiration, as in the calcium-chloride treatment. With my experimental plants, the detachment of the treated leaf stems occurred as rapidly and as slowly as in those without gypsum. In some cases, I even observed an appreciable retardation of the leaf-stem separation by twenty-four to forty-eight hours as consequence of the plaster coating of the mutilation. It therefore remains an open question whether the gypsum lump promoted or hindered transpiration through the capillaries of the Coleus stems.

12. Motion in space increases transpiration of the plant organs. After blade removal, Coleus stems were connected with a clock work and lever system so that they quivered gently but steadily. Those stems not subjected to motion became detached at the same time as those in motion. I noted occasionally that a stem connected to the system of motion became detached somewhat later than the opposite stem of the same pair which participated in the movements but was not exposed to any mechanical deformation. That mechanical effects may interfere with processes of tissue formation is not surprising and familiar from other observations (Ref. 6).

The importance of transpiration for leaf fall was demonstrated through numerous observations by Wiesner. Coleus also belongs among those plants in which detachment of the leaves from their axes can be accelerated by diminishing transpiration (Ref. 7).

Detailed investigation of the fact that intact leaves of Coleus drop off more quickly and in greater number in moist than in dry air is not a part of our problem. Important in its evaluation is the fact that such organs which have in no way near a similar intense transpiration as the leaf blades, "jump off" in moist air. Partially clipped short shoots of Populus pyramidalis dropped off within a few days in a vaporous atmosphere (Ref. 8). The action of the moist air apparently is due to the formation, under its influence, of hydrophile tissues at the point of abscission which produce the detachment. It is very likely that the same conditions prevail also in the spontaneous detachment of many intact leaves where, in the latter also, the essential is not the weak flow of transpiration or the insufficient supply with salts of the blades but the water saturation of the cells at the base of the leaf stem inducing hypertrophic growth.

There is the further question whether the dropping of the stems after resection of the blades is a consequence of the reduced transpiration and the diminished intensity of the flow of transpiration through the leaf stem. The test described above led me to the conclusion that other factors must be controlling in the process of leaf detachment observed by us.

III. The question of the nature of these controlling factors can presently not be answered. In my opinion, it would be obvious to think of chemical correlations existing between blade, stem and axis with which the elimination of the blade interferes. Whether the blade forms substances which prevent the formation of an abscission layer, or whether substances are furnished by the stem or by the axis which induce formation of an abscission layer but are made inactive in the young and intact leaf by specific factors from the blade, or whether more complicated chemical correlations exists, is not yet ripe for discussion.

To turn to specific factors of the blade in our hypothesis, is suggested by the observation that even small areas of the blade measuring less than one cm^2 are still able to "protect" the leaf. Stems allowed to retain a small remainder of the blade are preserved whereas the completely debladed stems become detached very soon. However, it was shown particularly clearly with green and/or green-white varieties

that the stems of aging leaves drop, even then when small remainders of the blade are retained, as quickly or almost as quickly as those completely debladed (cf. Test 6 above). In young but fully mature leaves, on the other hand, stems retaining a small remainder of the blade continue to be preserved for days and weeks even then when -- as was shown earlier already (Test 2) -- the remaining blade section is no longer capable of photosynthesis.

Similar observations as on Coleus plants can be made also on plants of other families. As far as I know, however, the difference in behavior of completely or partially debladed stems is never as striking as in Coleus. The latter either require a larger remaining blade section if the stems are to be preserved, or else the interval during which the blade remainder is still able to preserve the stem, is less (tests with Impatiens parviflora where the leaves furnish relatively irregular findings, and the observations of Ref. 9 on Brassica oleracea).

13. Completely debladed or partially debladed leaves of Coleus react basically different. Differences of degree can be observed if the stems themselves are shortened more or less. Detachment takes place as much earlier as the remaining stump of the leaf stem is shorter.

14. In order to determine whether the distance of the injury from the point of abscission is the controlling factor, long leaf-stems were imperfectly halved by a longitudinal section. These longitudinal injuries approached close to the point of insertion of the stems. This did not accelerate the process of detachment.

On the influence and location of the injury on the process of leaf fall, the next series of tests also furnished only negative information.

15. The interruption of the paths of conduction was achieved by making wedge-like cuts on two opposite sides or cutting out wedge-like sections from leaf-stems of selected robust specimens with thick stems.

The stems obviously lost their structural strength and consequently were provided with attached wooden splints prior to the operation. Red specimens were preferred because of their strong growth. Comparison between debladed stems and leaves with cut stems was made possible by the different treatment of the leaves of one pair. The debladed stems dropped from the experimental plants two to three days after the intervention whereas the leaves with cut and splinted stems remained firmly attached to the axis appreciably longer, generally until the end of the interval of observation, i.e. ten days after the operation.

Some leaves were treated so that their blade was removed eight to ten days after the cutting intervention. One of the stems became detached already twelve hours after this second intervention, the next dropped twenty-four hours later and others followed forty-eight and seventy-two hours later.

Green and/or yellow-green specimens disclosed less definite regularity in the behavior of the cut leaf stems.

16. I was unsuccessful in influencing the reaction of debladed stems by grafting. Cut leaves of the same specimen, leaves or buds from another plant of the same variety were grafted to robust stem stumps. The process of detachment was not delayed by such measures.

The tests furnish only negative information on the properties of the substances assumed in the hypothesis of the chemical correlations discussed. The hypothetical substances are not identical with those generated everywhere on injuries of living plant organs and the latter appear to be of considerable importance for the formation of abnormal tissue (Ref. 10). Moreover, the action of such substances is not linked to the existence of intact paths of conduction. In addition, they are still effective even where photosynthesis has not been possible for several days.

I cannot attempt to draw conclusions from the findings of Test No. 16 although the experiments were performed with the same result under different circumstances -- in the Botonical Gardens of Kiel and Bonn -- for several years.

Footnotes and Bibliography

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2 - Kuster, Pathological Anatomy of Plants. 2d Edition. Jena 1916. 424.

3 - Kuster, Gallnuts of Plants. Leipzig 1911. 358.

4 - Cf. Fitting, 1911 and elsewhere. Mirabilis jalapa also belongs to those plants which react very quickly by spontaneous decomposition of shoots through the action of laboratory air (within twelve hours), by decomposition of the younger parts of the axes in the individual internodes.

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